DANISH RESEARCH UNIT FOR INDUSTRIAL DYNAMICS

DRUID Working Paper No 04-05

Population Thinking and Evolutionary Economic Analysis: Exploring Marshall's Fable of Trees

by

Esben Sloth Andersen

Population Thinking and Evolutionary Economic Analysis: Exploring Marshall's Fable of Trees

Esben Sloth Andersen

DRUID and IKE, Aalborg University
E-mail: esa@business.aau.dk
Web: www.business.aau.dk/evolution/esa

Abstract:
It is increasingly recognised that population thinking is a basic characteristic of evolutionary economics. By taking its starting point in what is here called Marshall's fable of the trees, the paper demonstrates that there are several forms of population thinking. The most basic form is intra-population thinking for single populations, and this thinking easily extends to structured populations, where selection takes place at several levels. But there is also a need of applying inter-population thinking to the co-evolution of populations and intra-to-inter population thinking to the emergence of new populations. To transform these forms of population thinking into evolutionary analyses, there is a need of simple analytical tools. The paper emphasises a simple and basic tool for population thinking – Price's equation. This little known equation provides a surprisingly powerful tool for the partitioning of overall evolutionary change into a selection effect and what may be called an innovation effect. This partitioning serves as a means of accounting for evolution and as a starting point for the explanation of evolution. The applications of Price's equation cover relatively short-term evolutionary change within individual industries as well as the study of more complexly structured populations of firms. It also, to some extent, helps to understand the effects of co-evolution between populations and the emergence of new populations.

Key words: Population thinking, Alfred Marshall, statistical analysis of economic evolution, Price's equation, multi-level selection
JEL Codes: O30, O40

ISBN 87-7873-155--0

Population thinking and evolutionary economic analysis: Exploring Marshall's fable of the trees

Esben Sloth Andersen

> The economist needs the three great intellectual facilities, perception, imagination and reason : and most of all he needs imagination[.] —Marshall (1961, 43)

1. An approach to economic evolution

Although many contributors to economic thought and analysis have been 'verging on the high theme of economic progress' (Marshall, 1961, 460), the modern forms of evolutionary economics did not start to emerge before about 30 years ago (Witt, 1993). Even from this start, modern evolutionary economics has encompassed different approaches. They range from very general analyses of evolutionary games to specific studies of industrial dynamics, and the diversity has significantly increased over the years (Nelson, 1995; Dopfer, 2001; Potts, 2000; Foster and Metcalfe, 2001). So we are forced to ask what—if anything—is common for all these diverse studies of economic evolution.

The present paper suggests that an important part of the actual and potential unity is found in the basic ways we think about economic evolution and in the analytic tools we apply to sharpen this thinking. Since evolutionary thinking and its analytic tools have not yet reached maturity, a simple survey does little to find and promote unity. Instead, we have to reconstruct and systematise evolutionary thought and the related tools, so the required effort in evolutionary economics may be compared with what Samuelson (1983) did for neoclassical economics in his *Foundations of Economic Analysis*. Like Samuelson, we need to find common denominators beneath the highly diverse surface of the literature. We may even find some room for a comparative static analysis of evolution. Our study will lead to results that are different from those of Samuelson, however. The reason is that while his neoclassical analysis is based on substantively rational agents and tends to be performed in terms of representative agents, evolutionary economic analysis is based on boundedly rational agents and takes the form of population thinking.

Theoretical analysis has revealed that the most important prerequisite for evolutionary economic theorising is to take serious the differences that exist within and between populations of economic agents. This may seem a trivial requirement, but in practice it is not at all easy to perform this kind of analysis. Many have learnt to think in terms of statistical 'populations' when analysing the significance of empirical data, but it is less common to use the changing statistical properties of real populations to obtain a basic understanding of their evolution. Instead, there is a widespread tendency to treat such real populations as classes that can be characterised by a few common characteristics. Since Plato, there have actually been standard philosophical arguments for abstracting from the myriad of 'superficial' variations in order to concentrate on the underlying 'idea' or 'type' that basically characterise the population. But this typological thinking is a major obstacle for an adequate treatment of evolution. Instead we need a population thinking that means that we deal with heterogeneous populations and to consider outliers as even more important than normal agents (Mayr, 1976; Metcalfe, 2001). This heterogeneity of populations is upheld by the behavioural inertia that characterises boundedly rational agents. If we study the distribution of behaviour (like strategy or productivity) in such a population, we normally observe that this distribution evolve over time. We also recognise that this evolution may be ascribed to two main forces. Selection is the force that implies that firms with different values of the characteristic have different growth rates. Thus selection presupposes variance with respect to a particular characteristic, and this characteristic must be important in each member's environment (including the other members of the population). Selection means that the mean value of the characteristic of the population will change. But this mean may also change because of innovation, imitation, learning and random drift. The latter factors of change may be grouped under the heading of innovation and they can, at least conceptually, be distinguished from selection.

Even from this short account of population thinking, it becomes obvious that this form of thinking has a statistical orientation. This fact is a source of both the unity and the difficulties of modern evolutionary economics. We have to apply some sort of statistical analysis in any kind of evolutionary study—from the evolution that takes place within a large firm via evolution of an industry to evolution at the regional, national and global levels. In all cases, we have to specify populations, behavioural characteristics, and the changing distributions of these characteristics. Whether we like it or not, we thus see that statistics enter even at the ground level of our thinking, where we define what to look for. The problem here is that few are accustomed to this kind of statistical thinking—partly because has poor support from commonly known analytic tools. To promote the unity of evolutionary economics there is thus a need for providing basic tools for population analysis. The potential of such tools is not only to unify different theoretical approaches but also to unify theoretical and empirical analyses of evolution.

The tools that support population thinking are to a large extent available, but they have mainly been developed within evolutionary biology. Therefore, there is a need to consider to which extent these tools are not only relevant for evolutionary biology but also for the study all other forms of evolution. That this is actually the case has become increasingly clear (Frank, 1998). It was R. A. Fisher (1999) who formulated the foundations for general evolutionary analysis through his combined efforts of developing modern statistics and modern evolutionary analysis. These foundations were largely formulated as a general theory of selection. At the very core of this theory is Fisher's so-called fundamental theorem of natural selection that says that the speed of evolutionary change is determined by the behavioural variance within a population. Fisher's immediate topic was biological evolution, but his analysis has full generality. He was actually proposing to treat selection in terms of what has later been called replicator dynamics or distance-from-mean dynamics. Thus the biologically oriented Fisher theorem may be seen as the application of a general Fisher Principle that is relevant for all forms of evolutionary processes (Metcalfe, 1994; 1998). However, Fisher's analysis is excluding what in the present paper is called localised innovation. Therefore, his equations do not cover the general case in which this phenomenon is present to a smaller or larger degree. George R. Price (1970; 1972a) solved this problem by developing a general method for partitioning of evolution. Thereby he not only clarified Fisher's main result about natural selection (Price, 1972b) and helped to lay the foundation for evolutionary game theory (Maynard Smith and Price, 1973). He also developed a general and very fruitful decomposition of *any* evolutionary change, and thereby he formulated the core of a general evolutionary analysis (Frank 1995; 1998).

The simple Price equation serves to formalise what may be called *intra-population thinking* by focussing the attention on selection and localised innovation. His analysis is very basic and it has, to some extent, been rediscovered in Metcalfe's (1998; 2001) statistically oriented evolutionary economics and even in Nelson and Winter's (1982) pioneering contribution. However, the historical and statistical study of real processes of economic evolution is confronted with the problem of defining the units of selection. Since these units can both be national economies, regional industries, corporations, plants, work groups and individual employees, there is obviously a need to move from simple intra-population thinking to *multi-level population thinking*. Somewhat surprisingly, Price's approach can immediately be applied to the formalisation of the thinking in terms of multiple levels of selection. Thereby the approach serves to overcome the controversy within evolutionary biology between the majority view that only individual organisms are selected and the minority view that emphasises group-level selection (Hamilton, 1996; Frank, 1998). But Price's method of analysis is even more helpful in evolutionary economics. Here we simply start by partitioning of aggregate evolutionary change in terms of higher-level units (like corporations). Thereby we obtain a selection effect and a preliminary innovation effect. The preliminary innovation effect can be partitioned in terms of Price's equation. Thereby it becomes clear that it includes both selection within the units (e.g. selection between plants) and a more narrowly defined innovation effect. This analysis of the innovation effect can go on until we reach units of selection with no meaningful intra-unit selection. Obviously, it is not the same type of selection that takes place at the different levels of selection. At some levels the selection comes close to what biologists call natural selection and at other levels we may be dealing with conscious or artificial selection. But this is no problem for Price's approach that operates in terms of a fully general concept of selection.

The first beginnings of an evolutionary economic exploitation of the simple and the multi-level versions of Price's equation can be found in evolutionary game theory. Here Price's equation is used to analyse the emergence of cooperation in small to medium-sized human groups—irrespective of whether cooperative behaviour is genetically or culturally determined (Gintis, 2000, Ch. 11). This analysis immediately leads to the study of the emergence of the institutions (i.e. higher-level selection environments) that make it advantageous to perform the 'altruistic punishment' necessary to uphold a high level of cooperative behaviour (Gifford, 2000; Boyd et al., 2003). But the narrowly defined issues normally studied by evolutionary game theory may imply that the full generality of Price's approach is not recognised (Price, 1995; Knudsen, 2002). Here the empirically oriented evolutionary economics of the Nelson–Winter tradition may be more helpful. At the same time, the connection to relatively complex empirical studies makes clear a core characteristic of Price's equations for both simple and multi-level analysis: they are designed for the analysis of relatively short-term studies (as emphasised by Frank, 1998, Ch. 1). The short-term approach is necessary for keeping the selection pressures constant, and this cannot be assumed for long-term evolutionary processes.

There are two major reasons for the long-term change of selection pressures. First, selection pressures change with the changing size of the population. As long as the population is small compared to the carrying capacity of its environment, selection favours units that are quick in exploiting the possibilities. But as the population grows, the selection changes to favour units that are finely tuned to survive in a crowded environment. Second, the environment is to a large extent composed of other populations. In the long-term there is a co-evolution between the different populations, and this obviously co-evolution obviously changes selection pressures. For instance, an industry is competing and collaborating with other industries, and this interaction is changing over time. To handle both forms of density-dependent evolution, we need *inter-population thinking*. But this form of thinking is not directly supported by Price's approach. The delimitation of this approach should, however, be considered a useful feature and not a failure of the approach since it separates clearly the study of sort-term issues from the study of long-term issues. Thereby it serves to emphasise the urgent need for developing complementary tools for the study of long-term evolutionary change.

The paper starts in section 2 by applying a basic heuristic from economic folklore: it can all be found in Marshall. This is certainly true with respect to population thinking. But Marshall never fully developed this part of his thinking, so we have reconstruct it—e.g. from his famous analogy of the trees of a virgin forest and his account for industrial districts. These ideas can easily be expanded to cover all the different forms of population thinking. The core of the paper deals with these forms and the related tools. First we in section 3 deal with basic intra-population analysis for single populations, and this is followed up in section 4 by a short treatment of how this analysis can be extended to structured populations, where selection takes place at several levels. Then we in section 5 deal with the issues of co-evolution of populations and in section 6 with the emergence of new populations. Finally some conclusions are drawn. Thus, the ambition of the paper is to give a broad coverage of the forms of evolutionary thinking and the related tools.

2. Expanding Marshall's fable of the trees

In order to master evolutionary analysis, we have to overcome a trees-or-wood problem. On the one hand, we have to avoid the danger of not being able to see the evolving wood for all its constituent trees. For instance, each firm is unique and has its own environment, so it is not obvious how to delineate an 'industry' that is common to a set of firms. However, since evolution is a characteristic of a population rather than its individual members, this firm-oriented view means that we have dropped evolution. If we, on the other hand, emphasise the aggregate population, there us a danger of not being able to see the trees for the wood. We may, for instance, consider an industry as an aggregate, but then industrial evolution becomes a mysterious phenomenon with no micro foundation.

Population thinking overcomes the trees-or-wood problem by emphasising that the evolution of the aggregate characteristics of the wood is the outcome of mutation and selection of individual trees. Thus, the long-term emergence of an increased biomass per acre of woodland is the combined result of the emergence of trees with new productivity characteristics and the selection of trees that have supernormal productivities. Similarly, we may see market selection against firms with low productivity. However, to be sure that a population-level productivity increase is really due to evolution, we need to keep constant the age composition of the population. Otherwise, the productivity increase may just be due to the intrinsic productivity increase caused by the maturation of trees, or firms, as they grow larger. This will typically be the case in a forest after a large windfall and in a young industry. But in a large forest we will normally see the emergence of an equilibrated size distribution. This is the moral of Marshall's (1961, 315 f.) fable of the trees:

> [W]e may read a lesson from the young trees of the forest as they struggle upwards through the benumbing shade of their older rivals. Many succumb on the way, and a few only survive; those few become stronger with every year, they get a larger share of light and air with every increase of their height, and at last in their turn they tower above their neighbours, and seem as though they would grow on for ever, and for ever become stronger as they grow. But they do not. One tree will last longer in full vigour and attain a greater size than another; but sooner or later age tells on them all. Though the taller ones have a better access to light and air than their rivals, they gradually lose vitality; and one after another they give place to others, which, though of less material strength, have on their side the vigour of youth.

This famous quotation prepares the ground for the definition of a stationary forest, where we have forest-level equilibrium although no single tree is in equilibrium. Thus, such a stationary forest is 'full of movement' (p. 367), we may ignore the effect of the developmental mechanism since the age and size distributions do not change. We may even resolve the trees-or-forest problem by studying a single representative tree. This notion has an obvious meaning if all trees (or firms) are of equal size (p. 367):

> Of course we might assume that in our stationary state every business remained always of the same size, and with the same trade connection. But we need not go so far as that; it will suffice to suppose that firms rise and fall, but that the 'representative' firm remains always of about the same size, as does the representative tree of a virgin forest, and that therefore the economies resulting from its own resources are constant[.]

Although this stationary forest allows an abstraction from the developmental mechanism, it is still under influence of the evolutionary mechanism. Through this mechanism, many characteristics of the representative tree will change over time. This change may imply an increased size—like in the evolutionary arms race that has produced giant sequoia trees from herbs—but it also influences many other characteristics of the trees. Similarly, Marshall envisages that the representative firm transforms from a family firm to a corporation.

Marshal does not explore these evolutionary aspects of his version of the fable of the trees. The reason is that this fable is placed centrally in Marshall's (1961)

Principles of Economics, where he presents what I shall call the mechanical Marshall Mark I model of economic life. But both the developmental and the evolutionary mechanisms point beyond this model towards the ‘biological’ or evolutionary Marshall Mark II models, which were intended for the never published volume 2 of the *Principles*. So it is relevant to speculate about an expansion of the fable of the trees for evolutionary purposes, and it is not too difficult since Marshall filled his published volume with evolutionary thinking and presented additional suggestions in other works (Raffaeli, 2003; Arena and Quéré, 2003). These suggestions clearly demonstrate that the fable of the trees was designed as a bridge: it allowed the introduction of the concepts of equilibrium and the representative firms needed by Marshall Mark I, but it also allowed the further intra-population thinking of Marshall Mark II.

The present paper has no room for a reconstruction of Marshall Mark II, but several aspects of his evolutionary thinking are obvious enough to suggest an expansion of his version of the fable of the trees. From the very beginning is should, however, be remarked that Marshall was in serious lack of adequate analytical tools—even in handling a simplified version of his evolutionary equilibrium. Although Marshall (1961, 460 f.) excluded ‘substantive new inventions’ and only covered ‘those which may be expected to arise naturally out of adaptations of existing ideas’ and the developmental ‘forces of progress and decay’, he had to emphasise that

> ... such notions must be taken broadly. The attempt to make them precise over-reaches our strength. If we include in our account nearly all the conditions of real life, the problem is to heavy to be handled; if we select a few, then long-drawn-out and subtle reasonings with regard to them becomes scientific toys rather than engines for practical work.

These and other formulations demonstrate both Marshall’s lack of analytical tools and his unwillingness to publish his preliminary attempts with ‘scientific toys’. The present expansion of the fable of the trees serves to reveal some of these difficulties and start a search for reduced-form problems and ‘scientific toys’ to opens up the ‘high theme’ of economic evolution. More specifically, the present approach to population thinking suggests a decomposition of this theme into four sub-themes. Let us briefly consider them in relation to an extension of the fable of the trees.

The simple forest fable concentrates on the evolution of a population in a homogeneous selection environment. It avoids the developmental story—that was emphasised by Marshall—and concentrate on the evolutionary outcome of the ‘struggle’ between the trees, e.g. with respect to productivity. In principle, we may tell such a fable in terms of a representative firm, but to grasp the details of the evolutionary process, we need a full account for the distribution of the characteristics of the trees. To simplify further, we may just ask what happens between two points of time. From an evolutionary viewpoint, this boils down to two things. First, the trees that had initially different productivities may have shown differential growth rates due to what we shall call selection. Second, the individual trees may have mutated or innovated. Evolution in the forest is thereby a combination of a selection effect and an innovation effect. This useful analytical distinction does not necessarily imply that selection and innovation are independent. Thus, we can accommodate to Marshall’s preference for Lamarckian learning without excluding less flexible and more ‘Darwinian’ characteristics. We can see that this evolutionary story it is not too far from Marshall (1961, 355) from his emphasis on variation:

> Every locality has incidents of its own which affect in various ways the methods of arrangement of every class of business that is carried out on it : and even in the same place and the same trade no two persons pursuing the same aims will adopt exactly the same routes. The tendency to variation is a chief course of progress; and the abler are the undertakers in any trade the greater will this tendency be ... [I]n minor details the variations are numberless.

Thus, it is obvious that Marshallian competition is not perfect in the modern neoclassical sense and that there is plenty of material for the competitive struggle between the trees.

The clustered forest fable tries to grasp Marshall’s interest for industrial clustering (Marshall, 1961, Part IV, Ch. 10) in the simplest possible way. Although we, basically, stick to the story of a population in a homogeneous selection environment, we add the fact that near-by trees may influence each other in a positive way. In this setting, it is possible that a group of neighbouring trees takes over the whole forest. If for random reasons a group of strong trees lives near to each other, they may create a local environment that is favourable for both their own growth and that of their offspring. Thus, we will have a successful forest locality. The question is, of course, why the positive effects do not spread more widely. Here we probably have to include a natural segmentation of the location that hinders positive relationships between the clusters although it still allows one cluster to overshadow another cluster. As long as we accept this simplified story of the clustered forest, we may perform the same decomposition of evolution as for the simple forest. If we look at the whole forest, we find a selection effect and an 'innovation' effect. However, if we study the 'innovation' effect, we will find that some of it is due to the positive and mutual 'selection' of near-by trees. This 'selection' will by many evolutionary economists be called innovation, but there is a qualitative difference between the environmentally induced 'innovation' and the rest of the innovation effect.

The diversified forest fable brings us closer to both Marshall's thinking and to real forests. Here we operate with a forest composed by a number of different species that each form a population and together form a forest ecology. In such an ecology the different species are collaborating and competing in a very complex manner. For this reason we often concentrate on a single species while holding all other species constant. This is, of course, what Marshall did through the *ceteris paribus* clause of his partial equilibrium analysis (and what we implicitly have done in the fables of simple and clustered forests). Alternatively, we may like many ecologists study the interaction between species with unchanging characteristics. But in both cases we exclude the co-evolution between the different populations of trees. The purpose of the diversified forest fable is to overcome this exclusion of evolution without making the analysis unmanageable by including too many details. One strategy is to concentrate on the evolutionary relationship between one focal species and another species. There are many examples of cooperative evolution both in Marshall's general account for the inter-industrial division of labour and in his specific discussion of industrial districts, but the diversified jungle also includes a great many relationships that are partially competitive. In both cases, the first task is to understand how the relationship influences evolution within the focal species. Then we may turn our interest to evolution within the other species, and finally we might grasp the long-term co-evolution of the two species. To understand the whole network of co-evolutionary relationships is, of course, much harder. Even to keep the image of an evolving diversified forest in mind seems nearly impossible.

The diversifying forest fable is analytically somewhat more tractable. Here the task is to grasp how new species emerge in any forest. Thus, we may start from a simple forest with a single species and study how a new species emerge in such a forest. In general, such an emergence takes place by finding an unexploited or underexploited niche in the forest. Due to Marshall's deep interest in the increasing inter-firm division of labour, many of his niches imply symbiotic relationships to existing species. Let us consider parts of his long account for the emerging division of labour in the printing industry. Here Marshall (1961, 259) apparently starts from scratch:

> Everyone is familiar with the pioneer newspaper editor of newly settled districts of America, who sets up the type of his articles as he composes them; and with the aid of a boy prints off his sheets and distributes them to his scattered neighbours. When however the mystery of printing was new, the printer had to do all this for himself, and in addition to make all his own appliances. These are now provided for him by separate 'subsidiary' trades, from whom even the printer in the backwoods can obtain everything that he wants to use. But in spite of the assistance which it thus gets from outside, a large printing establishment has to find room for many different classes of workers within its walls.

The emphasis is here on two different situations for diversification. In the Wild West, we find a situation that appears well suited for the creation of new auxiliary species, but such species are already available due to the long-term evolution of printing. Thus, it is at the location where the new niche first becomes sufficiently large for a new species that it is most likely to emerge. This process of niche formation continues in the centres of growth of the printing industry, and Marshall is able to list many specialities. His division-of-labour approach, however, only covers some of the ways in which diversification of populations takes place, and he hardly provides any analytical tools for handling the process.

The four versions of the fable of the trees may be a good way of grasping some of the evolutionary problems that Marshall faced but never treated systematically. They, furthermore, give us a logical ordering of the tasks of evolutionary economic analysis—from the simpler to the more complex. But they do not hide the fact that Marshall gave up his attempts to formalise his evolutionary images. This question is whether modern evolutionary economics is able to move from fables and population thinking to systematic evolutionary analysis. In other words, are we today able to overcome the difficulties that a skilled economist and mathematician like Marshall could not handle?

3. The simple forest: Intra-population thinking

The breakthrough came with the *Genetical Theory of Natural Selection* by the geneticist and statistician R. A. Fisher (1999), who may be called the founding father of the statistical analysis of intra-population evolution (and of much of modern statistics!). Among his results, we shall concentrate on what may be called the Fisher principle (Metcalfe, 1998, Ch. 2). It is a generalised version of Fisher's (1999, 46) statement that '[t]he rate of increase of fitness of any species is equal to the genetic variance in fitness'. ' If we study a step-wise evolutionary process, we may reformulate his theorem in discrete terms. Let w_i be the fitness of an individual unit (organism), w the mean fitness of the population and Δw the change in mean fitness. Furthermore, let $\mathrm{Var}(w_i)$ be the population's variance of fitness (the reason for the non-standard subscript will become clear in section 3). Then the Fisher theorem says that

$$\Delta w = \mathrm{Var}(w_i). \tag{1}$$

This theorem describes a distance-from-mean dynamics, where the representation of a unit at the end of the period (its offspring) is determined by its relative fitness. Units with above-average fitness will increase their weight in the population, while units with below-average fitness have decreasing weight. The change in mean fitness is thus determined by the variance of unit-level fitness in the beginning of the period under study. Apparently, Fisher's theorem (1) is only about biological evolution, but his general formulation of selection and his inspiration from thermodynamics secured its general applicability. Thus general applicability may be emphasised by talking about the Fisher Principle (Metcalfe, 1994; 1998, Ch. 2), which serves as a starting point for the formalisation of population thinking. Especially, it helps us to recognise the enormous importance of statistical concepts—both in evolutionary theory and in the empirical study of evolution.

Fisher's work started—like the work of e.g. Nelson and Winter (1982)—from statistics of populations and their change. The Fisher theorem states that if selection favours the degree to which a particular property/trait is present in the individuals, then the rate of change of the mean value of this property is proportional to the variance of the property within the population. Thus, we have to define the properties that are selected for, measure their variance, study the strength of the selective forces, and follow the consequences at the aggregate population level. It is, however, important not to make this analysis in terms of a pure selection process. By doing so we ignore that the change in the property is not only due to selection but also to other causes of improvement and deterioration. This problem was mentioned by Fisher, but since it was not included in his formal analysis, it has much too often been forgotten. Metcalfe (1998) suggests that we should emphasise the Fisher principle (which includes the broader issues) rather than the narrow Fisher theorem. This task is, however, solved elegantly by G. R. Price, who was also the co-founder of evolutionary game theory (Maynard Smith and Price, 1973).

To overcome some of the ambiguities of Fisher's formulation of his theorem, Price (1970; 1972a) made a decomposition of the evolutionary change that included not only the effect of selection but also the effect of causes that increase variation. Price's equation (or formula) is not easy to understand, so even though it resolves many of Fisher's problems, it is often used in a delimited version is of less importance. Frank (1995; 1997; 1998) has been a major contributor to the development and diffusion of the full version of Price's decomposition of evolutionary change. His contributions demonstrate that a large number of evolutionary problems can be clarified by means of Price's equation. They also make clear that many researchers have been moving in the same direction as Price without noticing the full generality of their results and their relationship to Price. This fact is emphasised by Metcalfe (2002, 90) 'For some years now evolutionary economists have been using the Price equation without realising it.' This statement holds for Metcalfe's (1998; 2001) own important contributions to theoretical evolutionary economics, but it has also some truth for Nelson and Winter's (1982) pioneering contributions to evolutionary economics. A few have made the same discovery as Metcalfe. Thus, several game theorists have begun to apply Price's equation (cf. Gintis, 2000, 267–268), and Knudsen (2002) have used both the equation and Price's general account for selection to rethink the role of habits and routines in theories of economic evolution.

To illustrate the functioning of Price's form of intra-population thinking, it is easiest to deal with an evolutionary process that moves in discrete steps—like agricultural production, where a new generation of output is brought to the market every year. Most evolutionary games and most neo-Schumpeterian models are of this type. For such cases, it is possible to make a simple analysis of evolutionary change from one period to another period. The same analysis can actually be applied to any discrete-step evolutionary process in biology, economics, and elsewhere. This analysis appears very different from the widespread approach of replicator equations (Silverberg, 1988; Hofbauer and Sigmund, 1998), where we study the change of population shares of (groups of) agents with different properties, but the two approaches are actually complementary (Page and Nowak, 2002). However, the present discussion follows Fisher and Price in concentrating on the change of the mean of a property of the population.

In the case of the simplest evolutionary version of the Prisoner's Dilemma game the obvious property is the strategy. Here we study the frequency of players with the cooperative strategy in the two periods and find the change in this frequency. Similarly, we may take the Nelson–Winter model in which we measure the mean productivity in the population of firms in the two periods and calculate the change in this mean productivity. Price's equation may also be used on data collected from a real population of firms or households. Presently we, however, shall work with simple models.

When we try to explain the evolution of a mean characteristic, we have the problem that it might be caused by many forces. It is, nevertheless, possible to decompose the change in the mean characteristic into two effects of which at least the first (the selection effect) is easy to understand. The second (which in this paper is called the innovation effect) is more difficult to grasp since its meaning depends on the type of evolution under study. However, a partitioning into these two effects is possible for any evolutionary change, so it may e.g. be applied to change in an evolutionary game or in the Nelson–Winter model. For these and any other evolutionary process, Price's equation states that

$$\text{Total change} \; = \; \text{Selection effect} + \text{'Innovation' effect.}$$

This verbal description of Price's equation gives a first impression of the elements of evolutionary change, but it cannot be fully understood without a little formal analysis. To decompose evolutionary change we need a study the individual members of a population a two points of time, where we denote variable values for the first period with their ordinary names and variable values for the second period by adding primes. The members that we study can either be individuals or groups of individuals. To perform the analysis, we need to operate in terms of several variables for both these members and the aggregate population. Let us gradually move through these variables before we restate the verbal equation in formal terms.

For each member of the population we need to obtain information on four variables. The first is the characteristic value z_i. In the simple Nelson–Winter model z_i is the productivity of a firm's capital stock. The second variable is the change of this productivity between the two periods Δz_i. The third variable is the population share s_i. In the Nelson–Winter model—where the underlying population may be said to consist of machines—this variable is a firm's capital share s_i. The fourth variable is the reproduction coefficient w_i, which is simply one plus the growth rate. If we multiply the first-period size of a member by its reproduction coefficient, we obtain the size in the next period. Given this information about the members of the population, we study additional population-level information in order to explain the change of the mean productivity Δz.

Table 1: Core statistics.

Variable	Description	Definition
s_i	population share of entity *i*	
z	mean value of characteristic	$\sum s_i z_i$
$\text{Var}(z_i)$	variance of characteristics	$\sum s_i (z_i - z)^2$
w	mean reproduction coefficient	$\sum s_i w_i$
$\text{Cov}(w_i, z_i)$	covariance of reproduction coefficients and characteristics	$\sum s_i (w_i - w)(z_i - z)$
$\beta(w_i, z_i)$	regression of reproduction coefficients on characteristics	$\text{Cov}(w_i, z_i) / \text{Var}(z_i)$
$\text{E}(w_i \Delta z_i)$	expected value of change in characteristics in the end population	$\sum s_i w_i \Delta z_i$

To study the selection effect we need basic population-level statistics (see table 1). Here it is useful to start from the regression coefficient of reproduction on productivity, which in this paper is denoted by $\beta(w_i, z_i)$. This regression coefficient shows the degree to which selection exploits differential productivities. Normally we deal with partial regression coefficients, but in the present discussion we shall operate as if productivity is the only determinant of the reproduction coefficient. Thus its meaning can be caught by considering the linear relationship

$$w_i = \alpha + \beta(w_i, z_i)z_i + \text{ error.}$$

The next population variable is the variance of the productivities $\mathrm{Var}(z_i)$. The variance describes the differences on which selection operates. If $\mathrm{Var}(z_i) = 0$, selection cannot produce any change of mean productivity. Given non-zero values of both the regression coefficient and the variance, we have a contribution to observed change of mean productivity. The information on the regression coefficient and the variance may be replaced by the covariance between reproduction coefficients and productivities $\mathrm{Cov}(w_i, z_i) = \beta(w_i, z_i)\mathrm{Var}(z_i)$. Following Price, we may simply define selection in terms of this covariance (see below).

The study of the innovation effect starts from firm-level change in productivity Δz_i. The effect of this change on mean productivity is dependent on the firms' capacity shares in the second period, so we need to introduce the reproduction coefficients (since $s_i' = s_i w_i / w$). The total size of the effect is the mean or the expected value of all the firm-level contributions to the innovation effect, i.e. $\mathrm{E}(w_i \Delta z_i)$. According to this definition of 'innovation', we are obviously dealing with change in productivity that may occur for a variety of reasons. Thus the innovation effect of evolutionary economics comprises innovation in the ordinary sense, imitation, learning, etc.

Given the above definitions, we can readily understand the two elements of Price's decomposition of evolutionary change with respect to e.g. a Nelson–Winter model. Price's equation states that mean productivity change

$$\Delta z = \frac{\mathrm{Cov}(w_i, z_i)}{w} + \frac{\mathrm{E}(w_i \Delta z_i)}{w} = \frac{\beta(w_i, z_i)\mathrm{Var}(z_i)}{w} + \frac{\mathrm{E}(w_i \Delta z_i)}{w}. \tag{2}$$

Equation (2) is an identity. Given some experience in elementary statistics, the derivation is fairly simple (see Andersen, 2003b). The fact that Price's equation is an identity means that it holds for any change in a characteristic, and thus also for productivity change.

It is often convenient to formulate Price's equation in a slightly modified version, where

$$w\Delta z = \underbrace{\mathrm{Cov}(w_i, z_i)}_{\text{Selection effect}} + \underbrace{\mathrm{E}(w_i \Delta z_i)}_{\text{Innovation effect}}. \tag{3}$$

Here the left hand side describes the change in characteristic weighted by the mean reproduction coefficient of the population. In this case, the definition of the selection effect and the imitation effect is particularly simple. Furthermore, it should be noted that the left hand side is structurally similar to the contents of the expectation term ($w_i \Delta z_i$). This means that Price's equation can be used to expand itself (see section 4).

Equation (3) shows that short-term evolutionary change of e.g. productivity is determined by two effects. The first is the selection effect that exploits the weighted variance of the productivities. If this variance is large, then mean productivity may increase quickly. The effectiveness of this selection is influenced by the degree to which the relative reproduction coefficients of firms reflect their productivities, and this degree is measured by linear regression as we have already discussed. Thus, selection efficiency is an empirical question that we have to confront for each time step of the evolutionary process. The second effect is the innovation effect. To see why this name is appropriate in the Nelson–Winter context, we have to consider the meaning of $\mathrm{E}(w_i \Delta z_i)$. If there is no change in the productivity of any of the individual firms, then the sum is zero. Why should productivity change at the firm level be different from zero? There are, of course, many potential reasons for both negative and positive values, but in the present context we shall concentrate of the knowledge issue. Here productivity change may be positive because of innovation, imitation or learning processes. It might be negative because the firm does not have an effective system of reproduction of its knowledge. The expected aggregate effects of both learning and forgetting are, of course, influenced by the capacity shares of the firms.

In specific cases, Price's equation (3) may be simplified. If we study pure selection processes, the innovation effect is zero. This is obviously what is assumed to derive Fisher's theorem (1). To see the connection to Price's equation, we observe that the evolving characteristic is the reproduction coefficients themselves. Thus Fisher's theorem can be derived from the Price equation in the following way:

$$w\Delta w = \mathrm{Cov}(w_i, w_i) = \mathrm{Var}(w_i).$$

Hereby it is emphasised that Fisher is operating in relative terms, i.e. he works with $\mathrm{Var}(w_i / w)$. Furthermore, the selection process means that the variance taken in the first period is less than the variance we found for the second period. The reason is both due to the movement of mean productivity and changes in capacity shares: firms below the mean have become smaller while the mean has moved closer to the firms that increase their capacity share. If the regression coefficient is constant, then we will see a decrease in productivity change between the two periods. To avoid the 'retardation of change' we need to switch on the innovation effect. This not only gives a short-term effect on mean productivity change. It also provides new variance with which the selection mechanism can work.

Nelson and Winter made a similar study of a pure selection process—although they were explicitly working in terms of an evolving characteristic. On this background it is not surprising that they obtained the same result—in a somewhat roundabout manner.[1] By means of Price's equation the result is directly obtained. For all pure selection processes we find that the change of a characteristic than influences fitness is proportional to the variance of that characteristic. We also find that the selection process means that the variance in the first period is less than the variance we find for the second period. The reason is both due to the movement of mean productivity and changes in capacity shares: firms below the mean have become smaller while the mean has moved closer to the firms that increase their capacity share. To avoid the slowdown of change we need to switch on the innovation effect. This not only gives a short-term effect on mean productivity

[1] In a footnote Nelson and Winter (1982, 243) remarked that an '... analogue for Fisher's theorem in the present model is the proposition that the rate of reduction in industry average unit costs is equal to the share-weighted cross-sectional unit cost. This proposition is indeed a theorem under the assumptions of the present model, a fact we were led to verify by the parallel with Fisher's result'

change. It also provides new variance with which the selection mechanism can work in future periods. The same problem emerges in productivity studies like those reviewed by Bartelsman and Doms (2000). To compare the increasing number of studies that are based on longitudinal microdata, the authors emphasise a partitioning of aggregate productivity that has great similarity with, and are easily rewritten to, Price's equation. The advantage of doing so is that the evaluation of the data becomes immediately connected to core results of evolutionary economics.

An obvious application of Price's equation is to follow what happens in the evolution of the somewhat more complex Nelson–Winter model of Schumpeterian competition. If we start with many equal-sized firms, and if different productivities have already emerged, then there is a rather strong selection effect. This selection effect is, however, influenced by the rate of depreciation of capital. It reaches a maximum with a depreciation rate of unity, where all production in the next period is made by new capital. As the industry becomes more concentrated, the selection effect becomes weaker. The reason is that firms with large market shares show monopolistic investment restraint. For such firms a large productivity gain may even lead to negative investment. The reason is that these firms maximise their profits in this way, but this also mean that they some of the productivity differentials are not used to increase mean productivity of the industry. In these and other ways, Price's equation allows a quick analysis of the aggregate behaviour of Schumpeterian competition.

4. The clustered forest: Multi-level population thinking

Although the above presentation of Price's equation has primarily related to the evolution of industrial populations, this formula is an identity that can be used for the study of any kind of change in which selection has a role to play. The decomposition may also deal with more structured populations than an industry in which every firm competes directly against any other firm. Actually, Price's formula has found a primary area of use for the study of structured populations. The reason is that both in studies of biological and cultural evolution it has become obvious that the formula suggests an easy and general way to handle populations that have both a group level and an individual level. Thus it functions as a major tool for the study of social evolution—no matter whether 'social' relates to ants of humans and whether social behaviour is influences by genes, culture or economic institutions (cf. Frank, 1998).

In the first 15 years of its existence, Price's formula found few applications (Grafen, 1985, 38), but after that time it has won fairly widespread applications among evolutionary biologists and, more recently, among some evolutionary game theorists in economics (Gintis, 2000, Ch. 11). It is especially Frank (1998) that has demonstrated the broad applicability and the unifying power of Price's formula. For instance, it has in biology served to obtain a certain degree of reconciliation between the majority view of individual-level selection and the minority view that emphasises group-level selection (Sober and Wilson, 1998; Gould, 2002, Ch. 8). Hitherto, group-level selection has largely been used to explain the biological and cultural evolution of 'altruistic' behaviour that seems to be a necessity for the functioning of human societies. However, given that 'altruism' is a potential of *Homo sapiens* in small to medium-sized groups, then the group-level analysis may also help to explain several aspects of business organisation and the functioning of localised groups of firms.

Group-level analysis may be applied to the study of any population that are partitioned in a nested way. Take, for instance, the productivity studies reviewed by Bartelsman and Doms (2000). Here the plant is often taken as the unit of selection, but plants are connected to firms, and firms are often connected to national economies within the global economy. Thus we have to deal with selection of plants within firms, selection of firms within national economics, and selection of national economies within the global economy. Since the national level is increasingly blurred due to transnational firms, we might have to make separate studies of the selection of plants within firms and the selection of plants within national economies. But irrespectively of our partitioning of the overall system, there is an obvious need to study the different kinds of selection that takes place at the different levels.

Let us start with Marshall's (1949, Part IV, Ch. 10) well-known theory of industrial districts. This theory was based in the commonplace observation that many English cities and geographical areas were highly specialised around the production of a small set of goods and that they upheld this specialisation over long time spans. It is possible to apply two-level population thinking to analyse this phenomenon. To simplify we consider only a single industry of a competitive economy. We assume that this population can be decomposed into sub-populations, each of which lives in an industrial district. Thus, we have an industry that is structured into districts (indexed by *i*) that consist of firms (indexed by *ij*). To explore the functioning of such industrial districts, we shall start by expressing Price's equation for the group level of the population—like the districts. Thus we now interpret equation (3) as dealing with industrial districts within a national economy. This means that

$$w_i = \sum s_{ij} w_{ij},\ z_i = \sum s_{ij} z_{ij} \ \text{ and } \ \Delta z_i = \sum s_{ij} \Delta z_{ij}.$$

Given this interpretation, it is obvious that we may apply Price's equation (3) to the evolution that takes place within the industrial districts. For each district we find that

$$w_i \Delta z_i = \underbrace{\mathrm{Cov}(w_{ij}, z_{ij})}_{\text{Intra-district selection effect}} + \underbrace{\mathrm{E}(w_{ij} \Delta z_{ij})}_{\text{Intra-firm innovation effect}}. \tag{4}$$

If we insert equation (4) into equation (3) and split the overall expectation term, we find that

$$w \Delta z = \underbrace{\mathrm{Cov}(w_i, z_i)}_{\text{Inter-district selection effect}} + \underbrace{\mathrm{E}(\mathrm{Cov}(w_{ij}, z_{ij}))}_{\text{Intra-district selection effect}} + \underbrace{\mathrm{E}(\mathrm{E}(w_{ij} \Delta z_{ij}))}_{\text{Intra-firm innovation effect}}. \tag{5}$$

If we compare equation (5) with equation (3), we see that what was at the level of industrial districts considered an innovation effect is now partitioned into the expectation of the selection effects within the districts and the expectation of the more narrowly defined innovation effect within the firms. In other words, we study change of mean productivity at the national level in terms of three effects. First, there is selection between the districts of the industry. Here we can either directly use the covariance between district reproduction coefficients and district productivities or use the formulation with the regression coefficient and the variance of district productivities. Second, there is the expected value of the intra-district selection effects. If the mean of these effects is significant, it is due to the differences in the selection process in different districts. Third, there is the expected value of the innovation effects—first over firms and then over districts.

Until now, the grouping of firms has been attached to districts, and they may show up to have importance. But the grouping can be made in the most arbitrary way. For instance, we may apply Price's formula to groups defined by the first letter of the names of the firms. Thus, there must surely be many insignificant ways of grouping firms. The best is, of course, to use groupings to test theories. So the question is which kind of theory we should apply. Here the example of industrial districts points to Marshall's theory, but to cover broader issues we shall instead turn to theories of the evolution of cooperation. Such theories have not least been developed in evolutionary game theory—both in its formal version and in its computer-simulation-oriented version.

Another kind of theories that may be explored by multi-level population analysis have been developed in evolutionary game theory—both in its formal version and in its computer-simulation-oriented version. Let us think of the latter and start from Axelrod's (1990; 1997) work, which at an early point included collaboration with one of the most important researchers on social behaviour in biology (Axelrod and Hamilton, 1981; see also Hamilton, 1996). According to this approach, social life is seen as a series of Prisoner's Dilemma games. Here it is possible to collaborate and obtain a welfare gain, but the temptation to exploit a collaborator means that the dominant strategy is to defect. Since this holds for both players, the result is that no welfare gain is obtained. The apparent solution is to introduce repeated games, where each player remembers previous games and punish defectors (the tit-for-tat strategy). Unfortunately, this solution is fragile to errors and misunderstandings. Social life, furthermore, is hardly stable enough to make the tit-for-tat solution feasible in medium-sized or large populations. Instead the solution seems to be to consider social life as structured into groups that in some way or another exclude many defectors and where collaboration is so productive that the effects of the actions of the collaborators outweigh the negative influence of remaining defectors.

The analysis of this solution can be handles by Price's equation, from which we for convenience exclude the innovation effect. To prepare for the Price decomposition we define z as the frequency of collaborators in the overall population. Thus $1-z$ is the frequency of defectors. Furthermore, we define the reproduction coefficient of a player with a given strategy in the first period as the number of players (including himself) that have been persuaded to follow the strategy in the next period. This number is determined by the relative payoff of the strategy. In an unstructured population, the payoff of collaboration is defined to be below that of defectors, so it will die off. So what about a population structured in groups? Equation (5) holds for each group and the innovation effect is equal to zero. Thus we have that

$$w\Delta z = \underbrace{\mathrm{Cov}(w_{ij}, z_{ij})}_{\text{Inter-group selection effect}} + \underbrace{\mathrm{E}(\mathrm{Cov}(w_{ij}, z_{ij})}_{\text{Intra-group selection effect}}). \tag{6}$$

If we in equation (6) move w to the right hand side, we see that the equation is about change of frequency of collaborators in the overall population. This change is influenced by two effects. Take first the expectation term: the intra-group selection effect on the frequency of collaborators. This effect must be negative as long as there are mixed groups. To see this, remember that $\mathrm{Cov} = \beta \mathrm{Var}$. Consider the contributions to the variance group by group. In homogeneous groups (either collaborators or defectors), variance is zero. Given the assumptions of the Prisoner's Dilemma, the regression coefficient has to work against collaborators. So the intra-group selection effect is negative as long as there are mixed groups. Furthermore, any unprotected group of collaborators can be taken over by defectors.

In order to avoid that collaborators are driven out of the overall population, the inter-group selection effect must be positive, i.e. there must be a positive regression coefficient of reproduction on the frequency of collaborators at this level. Furthermore, the effect must be sufficient to outweigh the negative intra-group selection. Thus

$$\mathrm{Cov}(w_i, z_i) > -\mathrm{E}(\mathrm{Cov}(w_{ij}, z_{ij})).$$

The mechanism here is that a group's mean payoff increases as the number of collaborators increases. Thus, although the relative number of collaborators decreases in mixed groups, the absolute number of collaborators may increase because their groups increase significantly more than average.

Our simple analysis based on Price's equation does not allow a broader study of the problems involved in upholding a high frequency of collaborators in a population that interact according to the Prisoner's Dilemma. It is, however, obvious that the situation can be improved significantly of collaborators have the possibility of largely playing with other collaborators. One strategy for securing this is ‘altruistic punishment’ (Gintis, 2000, 271–278). This strategy implies that altruists punish defectors at a personal cost, while the benefit is gained by the group as a whole. Such punishment may imply that it does not pay to be a defector. But how can it pay to be such a kind of altruist? Price’s equation tells us so—if we reinterpret A as the frequency of this kind of altruists. Computer simulations appear to demonstrate that this mechanism might have been working for the altruistic propensities of humans (Boyd et al., 2003), but in the present context, it is more interesting to know whether we have an evolutionary mechanism that explains many of the phenomena of economic organisation. This seems indeed to be the case.

5. The diversified forest: Inter-population thinking

In the preceding sections, we have explored formal intra-population thinking and stretched it to its multi-level limits. But the analysis of evolutionary processes also requires that we are able to handle the interaction between different industries by means of inter-population thinking. For instance, we would like to know how a population of firms co-evolve with its customer population and how the functioning is of broad networks of co-evolutionary relationships between populations. Unfortunately, the requited form of thinking is more complex and less supported by formal tools than intra-population thinking. But this caveat should not lead to an abandonment of the study of crucial forms of economic evolution through the sole reliance on an evolutionary version of Marshall’s partial equilibrium method. Instead, we should confront co-evolution, and thereby we might even find that some of the more narrow tools are of great help. This has been demonstrated by e.g. Saviotti (1996; 2001) within the tradition of evolutionary replicator dynamic analysis. In relation to the present paper it should, however, be pointed out that the complementary tradition based on Price’s formula has been able to exploit its generality to handle aspects of surprisingly difficult issues.

The first thing to note is that interactions between populations are normally handled by formal tools that have a family relationship with replicator dynamics:

the Lotka–Volterra equations for interacting populations (Hofbauer and Sigmund, 1998, Part 1). But this tool was originally designed for dealing with the interaction between homogeneous populations. Thus, it was a non-evolutionary tool that has often been connected with typological thinking. This holds both for its economic and biological applications. Thereby the 'ecological' tradition was in sharp contrast with the intra-population tradition in both biology and economics, which has for a long time been based in evolutionary population thinking. This difference has, however, been bridged by evolutionary ecology (e.g. Pianka, 1999), which in the social sciences is e.g. covered by Hannan and Freeman (1989) and Carroll and Hannan (1999).

Even though the original differences have largely been overcome, there is still a serious difference between the two approaches. It concerns the assumptions about the density dependence of selection. Here the modern inter-population tradition is based on the assumption that the density of a population influences the selection among its members, just like the density of one population influences selection in other populations. In the evolutionary version of the famous predator–prey model, selection for many traits increases as an isolated population of prey grow toward its carrying capacity, while the density of predators represents a varying selection pressure on other traits. The intra-population tradition has traditionally abstracted from the density dependence of selection. The reason is partly that this tradition is engaged in analysing the selection for many properties within a single population. To simplify this analysis it is useful to hold selection pressure (e.g. in terms of predators) constant. The analysis of selection for many traits is also made easier if their relationships to selection are assumed to be additive. Therefore, this tradition tends to dislike complex interactions between properties. This is a useful strategy, but it tends to create the opinion that 'it is a bad mistake to think that the Fundamental Theorem actually holds in the real world' (Gintis, 2000, 197). This viewpoint is fully correct and founded in some of the deeper problems of the intra-population approach. But as it has been shown above there are several problems about the Fisher theorem that can be resolved.

However, with the help of the work of Frank (1998), Metcalfe (1998; 2001) and others, it is possible to avoid much of the controversy that relates to the Fisher theorem. First, it is easy to criticise Fisher's emphasis on variance, but actually he emphasises factors that are now formalised in the second of Price's effects. Second, the emphasis on selection and mutation with respect to a single property (here e.g. narrowly defined productivity) has led to the impression that evolutionary processes are relatively simple, but this is not the case. Actually, we ought to make Price decompositions for each of the huge number of properties that are selected for and that determine the (probabilistic) success of firms (and organisms). Third, the recursive expansion of Price's equation demonstrates that selection can take place at different levels. Thus, a bridge is created between theorists that emphasise 'individual selection' and theorists that concentrate on 'group selection'. This is done by emphasising that they cannot be taken as separate processes and that we can specify the conditions under which the inter-group selection is more important that the intra-group selection.

This defence of Price's version of the Fisher principle is not meant to say that it is well suited to handle all aspects of actual evolutionary processes. For instance, the introduction of density dependent selection may allow the coexistence of firms with different properties and different populations of firms. In the broad version Price's equation does not exclude e.g. density-dependent changes in the regression coefficients, but is does little to help us to think about them. The reason is that its basic trick here is to emphasise short-term evolutionary change in a more or less equilibrated situation. This strategy means that we can remove all the interaction effects from our replicator equations. As soon as we turn to long-run evolution, this simplification is neither formally correct nor likely to capture the real process of economic evolution. This issue is forcefully developed by Frank (1998), but his conclusion is that we should try to avoid the complex issues. Instead, he argues for the use of comparative static tools, where the major requirement is that populations change more quickly than their parameters. This conclusion is, however, hardly transferable to evolutionary economics that is still engaged in exploring the basic mechanisms of economic evolution.

Let us consider the density dependence of the reproduction coefficients w_i — first within a population and then with respect to interacting populations. As before populations are denoted by subscript *i* and the members of the populations by *ij*. For concreteness, we shall relate to the Nelson–Winter model. To get started, we shall initially switch off innovation and give all firms the same productivity.

Given these assumptions, there is neither a selection effect nor a real innovation effect. Thus, Price's equation (3) tells us that there is no productivity change. Nevertheless, the reproduction coefficients may show change from one period to the next. To see why, let us measure the size of the population by its capacity—e.g. the number of machines. Then we make a Price partitioning of the change of the mean reproduction coefficient of population *i*. The total change and the individual effects may be denoted

$$\Delta w_i = \Delta w_i^{\text{selection}} + \Delta w_i^{\text{innovation}}.$$

To specify the two effects, we simply reapply equation (3), but now we include the subscript *i* to indicate that we are dealing with several populations. Thus,

$$w_i \Delta w_i = \mathrm{Cov}(w_i, w_i) + \mathrm{E}(w_i \Delta w_i) = \mathrm{Var}(w_i) + \mathrm{E}(w_i \Delta w_i). \tag{7}$$

As earlier, the selection effect of equation (7) is straightforward. But since we have assumed that variance is zero, the selection effect is also zero. However, due to the explicit treatment of density dependence, we have to reconsider the meaning of the second effect. Since by assumption no innovation takes place, the change in the population's mean reproduction coefficient Δw_i is only due to density effects. So we may name it the 'environment effect' rather than the 'innovation effect'. But since the focus of the present postscript is on innovation, we shall stick to the name that is presently so confusing.

Seen from the viewpoint of a firm in industry *i*, its environment consists of other firms of the same industry, firms of other industries, and the resources that it exploits. To simplify the analysis, we assume that both intra-population competition and inter-population competition concern the exploitation of the same resource (e.g. a population of customers). This assumption implies that both the number of machines in population *i* (x_i) and the aggregate number of machines in all populations (x) contribute to the selection pressure on the individual firm. Let us start by considering the situation where population *i* is alone. In this case, we may apply the logistic equation to describe the situation. According to this equation, the level of crowding with respect to resource exploitation determines the populations' mean reproduction coefficient. As a small population of machines grows larger, crowding reduces the reproduction coefficient until the population reaches unity at the 'carrying capacity' of the resource. This is the density effect or interaction effect—determined by the squared number of population members. But the reproduction coefficient is also influenced by each member's intrinsic capability to grow.

The logistic equation applies change rates rather than reproduction coefficients. It is also most conveniently expressed in continuous time. It states that the change rate of the size of the population

$$\frac{\mathrm{d}\,x_i}{\mathrm{d}\,t} = r_i x_i - b_i x_i x_i = r_i x_i\left(1 - \frac{x_i}{K_i}\right), \tag{8}$$

where $K_i = r_i / b_i$. In this equation r_i is the maximum reproduction coefficient, which is found when N_i is very small. K_i is the steady state size of the population, which may be considered as the carrying capacity of the exploited resource with respect to population *i*. When this population size is reached, the change rate is zero and the reproduction coefficient is unity.

To give evolutionary meaning to the logistic equation (8), we have to remember that we are dealing with potentially heterogeneous firms. Thus, differential traits may imply that some firms show above-average reproduction coefficients in particular situations. When the population of machines is very small, individual firms that are organised in a way that allows them to expand quickly will have the highest reproduction coefficients. Thus, the frequency of such traits will increase, while other traits will be selected out of the industry. This is the *r*-selection of MacArthur and Wilson (2001). This selection regime becomes permanent if the population of machines is often reduced in size, and the industry thus has to restart its expansion. Otherwise, the population will move toward the carrying capacity of the resource, and here *K*-selection among the firms is predominant. This kind of selection favours firms with traits that increase their efficiency in exploiting the resource—like firms with quality products or complicated game strategies.

The simplest way of moving from the analysis of density dependence within a single population to the multi-population case is to assume that the total number of members of all populations ($x = \sum x_i$) influences the rate of change of each individual population. This assumption means that the capacity of all firms from all the industries have an equally negative influence on the reproduction coefficient of a particular firm. Thus, we may apply a simplified version of the Lotka–Volterra equations. In our simple competitive case, equation (8) only needs a minor modification to handle the multi-population case:

$$\frac{\mathrm{d}\,x_i}{\mathrm{d}\,t} = r_i x_i - b_i x_i x = r_i x_i \left(1 - \frac{x}{K_i}\right). \tag{9}$$

Compared with equation (8), the only novelty of equation (9) is that x_i / K_i has been replaced by x / K_i. But the consequence is significant. Now whole industries may have an average behaviour that gives them relatively high reproduction coefficients when the overall population density is small. But such *r*-strategy industries tend to do gradually more badly as the aggregate population density increases. If this expanding exploitation of the resource is not stopped by set-backs, then it is the relative sizes of the carrying capacities of the industries that determines their destiny. If industry *A* is adapted to *r*-selection and industry *B* is adapted to *K*-selection, then $K_B > K_A$. This means that when industry *A* has reached a zero change rate, industry *B* is still expanding. Thus, industry *A* will start to decrease and ultimately it will vanish. If the exploitation of the resource allows sufficiently stable populations, only the industry with the highest K_i will survive.

This short description of density-dependent selection is based on the relative stability of the population parameters (r_i and K_i), while no such assumption was made in Price's equation (7). Instead, this equation formally presupposes that we stick to short-term evolutionary change. In this way, it becomes a universal tool. When we move to density dependence and inter-population thinking, we need additional and less universal tools. But even here Price's equation may help to clarify the details of the evolutionary process. For instance, studies in terms of the logistic equation (8) and the Lotka–Volterra equation (9) tend to consider the behavioural variance as absent or given. But in real evolution, the second term of Price's equation (7) is including both an environment effect and an innovation effect. Thereby it suggests that the important thing when a set of populations starts to reach the individual carrying capacities is not only their given abilities to handle this situation. It is probably more important how they innovate. The effect of innovation on the change in mean reproduction coefficients will also have an effect on their saturation sizes K_i. Thus, it is important to remember that these 'parameters' are really variables. Therefore, we should include into our study the changes of the carrying capacities ΔK_i. It appears plausible that the industry that has the best innovative performance under *K*-selection will be the one that survive. To fixate this issue, it is convenient to call the adaptation to a crowded situation *K*-innovation.

The short discussion of *r*-selection and *K*-selection is in line with the postscript's general preference for simple analytic tools. Such tools tend to clarify many discussions and they suggest empirical questions (e.g. the measurement of r_i and K_i in different industries, and the study of *K*-innovation). But it is, of course, important to know whether the simple tools can handle complex issues. Ultimately, we have to cope in some way of another with the evolutionary consequences of the whole range of inter-industrial relationships. For instance, Schumpeter (1939) challenges us to handle the multiple ways in which the so-called 'railroadization of the world' changed economic structure during the nineteenth century (cf. Andersen, 2002). Here we obviously cannot perform the analysis by means of the truncated version of the Lotka–Volterra equation (9). In principle, we have to include the interaction coefficients between a number of industries and study the resulting complex dynamics. The question is, however, whether the inclusion of the detailed effects of the density of each industry on the densities of all the other industries will help us much. For instance, we have to drop the idea of using a single density variable like in equation (8), but we have to find other simplifications to avoid the analytical problem to become unmanageable. Schumpeter's idea of radical innovations might be the beginning of such a tool, but it is hard to see how it can become analytically operational. In the more complex setting it also becomes very hard to define K_i and other core parts of inter-population thinking. So even when we perform 'history-friendly modelling' (Malerba et al., 1999), we are forced to make harsh simplifications.

6. The diversifying forest: Intra-to-inter-population thinking

In the previous section, we only considered a small subset of the issues of inter-population thinking. The reason is that the tools that we have considered give insufficient support for this kind of analysis. What is missing is not least an understanding of why the different populations exist. To handle this question we may turn to intra-to-inter-population thinking. Here we study how and why new populations emerge out of old populations. This is a difficult study, and we may avoid it by assuming the emergence of new populations by sudden jumps. Such jumps characterise Schumpeter's (1934) theory of evolution based on radical innovations. In new growth theory, we find the same approach. Thus, Romer (1990) and Aghion and Howitt (1998) models novelty as new sectors in which monopolists produce intermediate goods. Such monopolists produce an increasing number of specialised inputs for the final goods sector. But the increasingly heterogeneous set of firms does not constitute a population. Instead there is one population in the final goods sector, where all firms are identical, and an increasing number of intermediate good producing 'populations', which each consists of one firm. So we are facing inter-population diversity but no intra-population variance. Furthermore, these firms have 'rational expectations' in the sense that they know the probability of obtaining an innovation and are able to calculate the optimal R&D effort (given that they are risk neutral).

Both the lack of population thinking in new growth theory and its assumption of substantive rationality exclude any analysis of the evolutionary process that in real economic life generates much of the observed economic growth. On this background it seems premature when Romer (1993, 559) suggests 'a natural division of labour in future research' between 'mainstream theorists and appreciative theorists' (p. 556). The former provide 'simple abstract models', while the latter provide 'aggregative statistical analysis and in-depth case studies' (p. 559). While Romer's diagnosis about the deficiencies of the formal tools of many theorists of economic evolution might be correct, his prescription has a big problem. It ignores the fact that the supposed suppliers of evidence—Romer mentions David, Fagerberg, Mokyr, Nelson (1993) and Rosenberg—are dealing with heterogeneous populations of boundedly rational agents that are not adequately formalised by the new growth theorists (cf. Andersen, 1999, 34–37).

The activity that that Nelson and Winter (1982, 45–48) call appreciative theorising is not least engaged in intra-to-inter-population thinking. Such theorising try to specify central facts about cases of economic evolution and then to modify or develop concepts and models that give an adequate account for these cases. The purpose is neither to prove the correctness of a given model nor to use the model for defining the relevant data. Thus, this approach might seem methodologically unsound. Appreciative theorising, however, has an obvious and important function: to bridge between abstract formal tools and the tasks and practices of empirically oriented industrial economists, economic historians, econometricians, etc. Recently, appreciative theorising has taken the form of relatively complex and 'history-friendly' models that bridge between empirically oriented studies and the more abstract models developed in or in relation to Nelson and Winter (1982). Malerba et al. (1999, 3–6) argue that while the first generation of neo-Schumpeterian evolutionary economic models has largely been characterised by an attempt to understand the basic logic of evolutionary processes, the major challenge presently is to develop a second generation of history-friendly models that can be of major help for empirical research in economics. This second generation of evolutionary models intends to reflect major stylised facts obtained by empirical researchers and that ends up not only by 'history-replication' but also with 'history-divergent' simulations. The immediate results presented by Malerba et al. (1999) and Malerba and Orsenigo (2001) suggest the need of emphasising the role of the diversity of demand, the emergence of new technologies and markets, and the role of entry and venture capital. Thus, the history-friendly models move from intra-population thinking to the more complex forms of population thinking—with an emphasis on what we here call intra-to-inter-population thinking.

While it is correct that intra-population thinking does not sufficiently support empirical studies of economic evolution, history-friendly modelling has to apply analytic tools that are adapted for intra-to-inter-population thinking. The same was the case in evolutionary biology, where the Fisher approach needs a complementary approach. Fisher's approach assumes that evolution takes place in huge populations and that sufficient time is available to select out individuals with subnormal fitness. Since not even Darwin had such a strong assumptions, Fisher may be characterised as a hyper-Darwinian. But his assumptions make it difficult to grasp intra-to-inter-population events. In this respect the formal modelling of Sewall Wright is much more flexible (Provine, 1986). Wright assumes that a population is placed in a fitness landscape that allows subpopulations with different properties emerge, and this assumption makes his approach relevant for empirical studies of subpopulations and the emergence of new species, like the ones performed by the pioneers of the neo-Darwinian synthesis (Mayr and Provine, 1980; Mayr, 1982). Here the properties of new species are not only determined by natural selection but also by random drift in small populations and by the random properties present in the subpopulations that found new species.

Underlying these results is the presence of a persistent amount of inheritable variance in natural populations, and this heterogeneity has shown to be present in empirical studies. Wright's emphasis on persistent heterogeneity is, however, contrary to Fisher's assumptions, and a Wright–Fisher controversy has been important for the development of evolutionary biology. This controversy sharpened by Kimura's theory of neutral evolution, but the study of molecular evolution has demonstrated that both sides of the neutralist–selectionist controversy have their part of the truth (Page and Homes, 1998, Ch. 7). In economic evolution there seems even less ground for a one-sided application of Fisher's assumptions. So Price's cautious development of the Fisher tradition might be of particular importance here.

An abstract study of the segmentation of the resources underlying the emergence of new populations and the continued existence of multiple populations is hardly satisfactory for empirical studies of economic evolution. So there is an urgent need to proceed to an economic evolutionary analysis of the most obvious source of segmentation in economic life: the division of labour and division of knowledge. Here there are two major strategies. The first strategy is to turn directly to the diversity of the market environment. The second strategy is to start from the inner diversity of the firms and/or households. We shall apply the second strategy by starting from multi-activity firms, so the task is to explain why and how individual activities become outsourced and coordinated by more-or-less clear-cut market mechanisms. Here we relate to the traditions in industrial economics and growth theory that trace back to the Smith-inspired ideas of Marshall (1961) and Young (1928). As we have already seen in Marshall's account for the printing trade, this tradition focus on the close relationship between the internal economies of firms and the external economies that arises from inter-firm specialisation with respect to production and knowledge creation.

Actually, Marshall's story of the printing trade is used by Young as an answer to the monopoly paradox that arose from Marshall's allowance into his system of economies of scale. There is no real paradox as long as we allow into our models the indefinite divisibility of production activities. This divisibility often makes a small well-focussed firm more productive than a large firm with a broad scope of activities. Although concentration is a real process, the trend is broken by the evolution of markets for gradually more intermediate goods that slowly undermine many of the industrial giants. Even in relation to such models one might, however, ask whether the limits of divisibility will be met 'at the end of the road'. In a Smithian context Richardson's (1975, 357) answer is 'that the end of the road may never be reached. ... For just as one set of activities was separable into a number of components, so each of these in turn become the field for a further division of labour.' The opening up of these possibilities is part of the evolutionary process itself: 'the very process of adaption, by increasing productivity and therefore market size, ensures that the adaptation is no longer appropriate to the opportunities it has itself created.' (Richardson, 1975, 358)

Let us reconsider Price's equation (3). Now we are dealing with mean productivity change with respect to the *i*th intermediate goods sector (Andersen, forthcoming). Before exchange has emerged in this sector, all producers of final output are engaged in this area of production. Thus, the reproduction coefficients are only weakly related to the productivities in this sector. This situation changes drastically with the emergence of a market for the intermediate good. Now the reproduction coefficients of the specialised firms become narrowly connected to their productivities in their speciality. Therefore, they tend to focus their research, and thus the innovation effect increases significantly. The consequence of their focus for the selection effect is more ambivalent. During a transition period, an increased variance emerges, so the increased regression coefficient has fuel on which to work. This transition period may, however, be rather short. Low productivity firms quickly shift from make to buy, and competition among specialised suppliers means yet another decrease of variance. It is, however, obvious that Price's formula gives us the discipline to analyse clearly all the stages.

The two-level Price equation (5) may provide further help in structuring the problems. Thus, we may distinguish between the group of firms that that produces the intermediate good for its own use and the group of specialised suppliers. But this equation also forces us to define precisely the selection levels of the economic system. As long as there is only a well-developed market for final goods, each firm is selected according to the mean of its activity-specific productivities. Thus, inter-firm selection concerns the firm as a whole, while intra-firm selection deals with individual activities. As soon as intermediate goods markets emerge, market selection works on (some of) the intra-firm activities, but this is also an area for intra-firm selection. So conflicts may emerge. When exchange has emerged, the generalist strategy implies relatively small productivity changes with respect to intermediate good i, while the specialist strategy secures a larger innovation effect because research is focussed.

7. Conclusion

This paper has dealt with population thinking from a particular viewpoint: the need of analytical tools. Although the situation is by far satisfactory, we have today significantly sharpened forms of population analysis to confront the problems of economic evolution in a more efficient manner than has hitherto been the case. To describe the new situation, we may apply Schumpeter's (1954, p. 39) formulation that 'a new apparatus poses and solves problems for which the older authors could hardly have found answers even if they had been aware of them.' The paper has demonstrated that population thinking is more multiform than normally recognised, and therefore it needs a complex analytical toolbox. However, an important theme of the paper was that Price's equation for the decomposition of evolutionary change is surprisingly powerful in supporting manifold tasks of evolutionary analysis. So although it apparently is a simple extension of the statistically oriented intra-population analysis in the tradition of R. A. Fisher, it may also help to transcend this tradition. The reason is partly that Price's equation avoids making strong assumptions about the kind of evolutionary processes that may be covered. This generality comes at a cost, namely that the equation is not sufficient to define a long-term path of evolutionary change. But this limitation should be seen as its strength rather than its weakness. For instance, it is far too easy to forget about the web of inter-population links when a system of replicator equations is projected into the long run. Price's equation helps us to be more modest by pointing to the many assumptions underlying such long-run dynamics. Presently, the major task for our understanding of economic evolution is, probably, to deepen our analysis of its shorter-term aspects.

Acknowledgements

This paper is a revised version of the paper that was presented at the DRUID Conference in Copenhagen, 12–14 June 2003. The paper's basic approach to population thinking owes much to Stan Metcalfe, who also suggested its author to have a closer look at Frank (1998). The paper crystallised due to the suggestion by Kiichiro Yagi to write a postscript for the Japanese edition of my book on evolutionary economics (Andersen, 2003a). Specific comments to my previous notes and papers by Thorbjørn Knudsen, Bengt-Åke Lundvall and Toke Reichstein have also proved fruitful. The usual disclaimer applies.

References

Aghion, P. and Howitt. P. (1998), *Endogenous Growth Theory*, Cambridge, Mass. and London: MIT Press.

Andersen, E. S. (1999), 'Multisectoral growth and national innovation systems', *Nordic Journal of Political Economy*, **25**, 33–52.

Andersen, E. S. (2002), 'Railroadization as Schumpeter's standard example of capitalist evolution: An evolutionary–ecological interpretation', *Industry and Innovation*, **9**, 41–78.

Andersen, E. S. (2003a), Population thinking and evolutionary economic analysis, Postscript for E. S. Andersen, *Evolutionary Economics: Post-Schumpeterian Contributions* [in Japanese], Tokyo: Springer. Forthcoming as a paper in *Evolutionary and Institutional Economics Review*, **1**.

Andersen, E. S. (2003b), A note on Price's equation for evolutionary economics: Derivation, interpretations, and simple applications, Department of Business Studies, Aalborg University.

Andersen, E. S. (forthcoming), 'Knowledges, specialisation and economic evolution: Modelling the evolving division of human time', in J. Foster and J. S. Metcalfe (eds.), *Frontiers of Evolutionary Economics*, Vol. 2, Cheltenham and Northampton, Mass., Elgar.

Arena, R. and Quéré, M. (2003), *The Economics of Alfred Marshall: Revisiting Marshall's Legacy*, Basingstoke and New York: Palgrave Macmillan.

Axelrod, R. (1990), *The Evolution of Cooperation*, reprint edn, London: Penguin.

Axelrod, R. (1997), *The Complexity of Cooperation*, Princeton, N.J.: Princeton University Press.

Axelrod, R. and Hamilton, W. D. (1981), 'The evolution of cooperation', *Science*, **211**, 1390–1396.

Bartelsman, E. J. and Doms, M. (2000), 'Understanding productivity: Lessons from longitudinal microdata', *Journal of Economic Literature*, **38**, 569–594.

Boyd, R., Gintis, H., Bowles, S., and Richerson, P. J. (2003), 'The evolution of altruistic punishment', *Proceedings of the National Academy of Sciences*, **100**, 3531–3535.

Carroll, G. R. and Hannan, M. T. (1999), *The Demography of Corporations and Industries*, Princeton, N.J.: Princeton University Press.

Dopfer, K. (ed.) (2001), *Evolutionary Economics: Program and Scope*, Vol. Boston, Mass., Kluwer.

Fisher, R. A. (1999), *The Genetical Theory of Natural Selection: A Complete Variorum Edition*. Oxford: Oxford University Press.

Foster, J. and Metcalfe, J. S. (eds) (2001), *Frontiers of Evolutionary Economics: Competition, Self-Organization and Innovation Policy*, Cheltenham and Northampton, Mass.: Elgar.

Frank, S. A. (1995), 'George Price's contributions to evolutionary genetics', *Journal of Theoretical Biology*, **175**, 373–388.

Frank, S. A. (1997), 'The Price equation, Fisher's fundamental theorem, kin selection, and causal analysis', *Evolution*, **51**, 1712–1729.

Frank, S. A. (1998), *Foundations of Social Evolution*, Princeton, N.J.: Princeton University Press.

Gifford, A. (2000), 'The bioeconomics of cooperation', *Journal of Bioeconomics*, **2**, 153–168.

Gintis, H. (2000), *Game Theory Evolving: A Problem-Centered Introduction to Modelling Strategic Behavior*, Princeton, N.J.: Princeton University Press.

Gould, S. J. (2002), *The Structure of Evolutionary Theory*, Cambridge, Mass. and London: Harvard University Press.

Grafen, Alan (1984), 'Natural selection, kin selection, and group selection', in J. R. Krebs and N. B. Davies (eds), *Behavioural Ecology: An Evolutionary Approach*, 2nd edn, Sunderland, Mass: Sinaur.

Hamilton, W. D. (1996), *The Narrow Roads of Gene Land: The Collected Papers of W. D. Hamilton*, Vol. 1, Oxford: Freeman.

Hannan, M. T., and Freeman, J. (1989), *Organizational Ecology*, Cambridge, Mass. and London: Harvard University Press.

Hofbauer, J. and Sigmund, K. (1998), *Evolutionary Games and Population Dynamics*, Cambridge: Cambridge University Press.

Knudsen, T. (2002), General Selection Theory and Economic Evolution: The Price Equation and the Genotype/Phenotype Distinction, manus to be published, Dept. of Marketing, University of Southern Denmark, Odense.

MacArthur, R. H. and Wilson, E. O. (2001), *The Theory of Island Biogeography*, reprint edn, Princeton, N.J. and Oxford: Princeton University Press.

Malerba, F., Nelson, R. R., Orsenigo, L., and Winter, S. G. (1999), '"History-friendly" models of industry evolution: The computer industry', *Industrial and Corporate Change*, **8**, 1–36.

Malerba, F. and Orsenigo, L. (2001), 'Innovation and market structure in the dynamics of the pharmaceutical industry and biotechnology: Towards a history friendly model', *Industrial and Corporate Change*, **11**, 667–703.

Marshall, A. (1961), *Principles of Economics,* 2 vols, C. W. Guillebaud's variorum edn, London: Macmillan.

Maynard Smith, J. and Price, G. R. (1973), 'The logic of animal conflict', *Nature*, **245**, 15–18.

Mayr, E. (1976), *Evolution and the Diversity of Life: Selected Essays*, Cambridge, Mass. and London: Belknap/Harvard University Press.

Mayr, E. (1982), *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*, Cambridge, Mass. and London: Harvard University Press.

Mayr, E. and Provine, W. B. (eds.) (1980), *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, Cambridge, Mass. and London, Harvard University Press.

Metcalfe, J. S. (1994), 'Competition, Fisher's Principle and Increasing Returns in the Selection Process', *Journal of Evolutionary Economics*, **4**, 327–346.

Metcalfe, J. S. (1998), *Evolutionary Economics and Creative Destruction*, London and New York: Routledge.

Metcalfe, J. S. (2001), Evolutionary approaches to population thinking and the problem of

growth and development, in Dopfer (2001).
Metcalfe, J. S. (2002), 'Book review: Steven A. Frank. 1998. Foundations of Social Evolution', *Journal of Bioeconomics*, **4**, 89–91.
Nelson, R. R. (ed.) (1993), *National Innovation Systems: A Comparative Analysis*, New York and Oxford: Oxford University Press.
Nelson, R. R. (1995), 'Recent evolutionary theorizing about economic change', *Journal of Economic Literature*, **33**, 48–90.
Nelson, R. R. and Winter, S. G. (1982), *An Evolutionary Theory of Economic Change*, Cambridge, Mass. and London: Harvard University Press.
Page, K. M. and Nowak, M. A. (2002), 'Unifying evolutionary dynamics', *Journal of Theoretical Biology*, **219**, 93–98.
Page, R. D. M., and Holmes, E. (1998), *Molecular Evolution: A Phylogenetic Approach*, Cambridge, Mass.: Blackwell.
Pianka, E. R. (1999), *Evolutionary Ecology*, 6th edn, New York: Harper & Row.
Potts, J. (2000), *The New Evolutionary Microeconomics: Complexity, Competence and Adaptive Behaviour*, Cheltenham: Elgar.
Price, G. R. (1970), 'Selection and covariance', *Nature*, **227**, 520–521.
Price, G. R. (1972a), 'Extension of covariance selection mathematics', *Annals of Human Genetics*, **35**, 485–490.
Price, G. R. (1972b), 'Fisher's "fundamental theorem" made clear', *Annals of Human Genetics*, **36**, 129–140.
Price, G. R. (1995), 'The nature of selection', *Journal of Theoretical Biology*, **175**, 389–396.
Provine, W. B. (1986), *Sewall Wright and Evolutionary Biology*, Chicago: University of Chicago Press.
Raffaeli, T. (2003), *Marshall's Evolutionary Economics*, London and New York: Routledge.
Richardson, G. B. (1975), 'Adam Smith on competition and increasing returns', in A. S. Skinner and T. Wilson (eds), *Essays on Adam Smith*, Oxford: Clarendon.
Romer, P. M. (1990), 'Endogenous technological change', *Journal of Political Economy*, **98**, S71–S102.
Romer, P. M. (1993), 'Idea gaps and object gaps in economic development', *Journal of Monetary Economics*, **32**, 543–573.
Samuelson, P. A. (1983), *Foundations of Economic Analysis*, enlarged edn, Cambridge, Mass. and London: Harvard Univesity Press.
Saviotti, P. P. (1996), *Technological Evolution, Variety and the Economy*, Aldershot: Elgar.
Saviotti, P. P. (2001), Considerations about a production system with qualitative change, in Foster and Metcalfe (2001).
Schumpeter, J. A. (1934), *The Theory of Economic Development: An Inquiry into Profits, Capital, Credit, Interest and the Business Cycle*, London: Oxford University Press.
Schumpeter, J. A. (1939), *Business Cycles: A Theoretical, Historical, and Statistical Analysis of the Capitalist Process,* 2 vols., New York and London: McGraw-Hill.
Schumpeter, J. A. (1954), *History of Economic Analysis*, ed. E. B. Schumpeter, London: Allen and Unwin.
Silverberg, G. (1988), Modelling economic dynamics and technical change: Mathematical approaches to self-organization and evolution, in G. Dosi, C. Freeman, R. R. Nelson, G. Silverberg and L. Soete (eds.) (1988), *Technical Change and Economic Theory*, London, Pinter.
Sober, E. and Wilson, D. S. (1998), *Unto Others: The Evolution and Psychology of Unselfish Behavior*, Cambridge, Mass. and London: Harvard University Press.
Witt, U. (ed.) (1993), *Evolutionary Economics*, Aldershot, Elgar.
Young, A. A. (1928), 'Increasing returns and economic progress', *Economic Journal*, **38**, 527–542.